RELATION OF LIGHT TO GROWTH OF PLANTS[1]

H. F. THUT AND W. E. LOOMIS

(WITH EIGHT FIGURES)

Plants grown in varying intensities of light from full sun to darkness show characteristic and well-known differences in growth and development. Much of this effect is frequently summed up in the phrase, "light retards growth," which has become almost axiomatic in plant physiology and has been used to explain certain types of phototropism as well as the varying growth rates of etiolated and unetiolated plants, etc. Like many other physiological axioms, the inhibiting effect of light was popularized by SACHS (**20**) who performed some of the early experiments indicating that plants may make most of their growth in darkness. SACHS recognized the several secondary effects of light on growth, but thought it directly inhibiting through some action on the growing regions.

Numerous other workers have considered light inhibiting for growth. PRANTL (**18**), POPP (**15**) and MCCALLA, WEIR and NEATBY (**13**) agree, at least in part, with SACHS. MASON (**12**) and POPP and BROWN (**16**) have stressed the action of ultraviolet rays in checking growth. MASON found that date frond elongation stopped soon after sunrise at Indio, California, and was not resumed until near sunset. Growth was resumed within a few minutes if the plants were covered during the day, but could be stopped under the cover or at night by the radiation of a quartz mercury arc. Tropical workers, BROWN and TRELEASE (**2**), COSTER (**3**), OSMASTON (**14**), PORTERFIELD (**17**) and TRELEASE (**21**), are generally agreed that daytime checks of plant growth are caused by internal water deficits in insolated plants rather than by any direct action of light. It might be assumed that the lower percentage of ultraviolet in the sunlight of the humid tropics accounted for their observations if it were not that LLOYD (**9**) was unable to find any direct effect of sunlight upon the growth of *Eriogonum nudum* at the Desert Laboratory at Tucson.

LOOMIS (**11**), working with potted maize plants in the greenhouse, concluded that the elongation of this plant was controlled by the temperature and the internal water supply of the plant and was not directly affected by light. Temperature is normally positively correlated with radiation, but water supplies within the meristematic tissues tend to be negatively correlated. The greenhouse glass would reduce the ultraviolet of sunlight by screening out the shorter and more active wavelengths. PRESCOTT (**19**), however, found that maize in the field in Egypt also made its greatest growth after sunrise in the morning and around sunset, with a midday drop that was accentuated by declining soil moisture percentages. There

[1] Paper no. J–1135 of the Journal series of the Iowa Agricultural Experiment Station. Project no. 678.

is thus a fairly general agreement among investigators that sunlight is not directly inhibitory for plant growth, although the verdict is not unanimous.

The present investigation was undertaken in the summer of 1939 to compare diurnal growth in the field with the earlier experiments on potted plants in the greenhouse, and to evaluate more accurately the various secondary effects of sunlight on growth. It was concerned with the effects of full sunlight on the growth of non-etiolated plants, so that the numerous complicated effects of light on plant form (**7**, **22**) have been ignored.

Results

Experiments with corn

Plants of the open pollinated, Station strain of Iodent (*Zea mays*) were grown on the Botany plots of the Agricultural Experiment Station at Ames, Iowa, in a deep, black, fertile loam. The increases in height of the unfolding, central leaves of vigorous maize plants 10 to 15 dm. tall were recorded as growth. This measurement includes size increases due to cell division and elongation at the base of the leaf, in the leaf sheath, and in varying numbers of elongating internodes below the leaf. Preliminary measurements showed, however, that closely agreeing results could be obtained from three or four of the younger leaves on any one plant.

Measurements were made by fastening a ring with adhesive tape to the leaf to be measured. Auxanometer needles, balanced to a uniform pull of 15 gm., were then hooked into the rings, and elongation read with a 5 to 1 magnification on a meter scale. Auxanometers were detached when not making readings to avoid disturbance by wind. Humidity readings were made with a sling psychrometer, and light readings with a Weston Sunlightmeter. Hygrothermograph records were obtained from a recording instrument in the field to check and supplement the direct readings. In most of the experiments with both maize and other plants, readings were taken at 2-hour intervals during the experiment. Growth was calculated as millimeters per hour for an average of six or more plants and recorded as the growth rate at the middle of the period. Light, temperature, and humidity readings were plotted as taken.

The curves of figure 1 show the results of a four-day experiment, started June 23, with plentiful soil moisture and rising temperatures. The first two days were sunny, as shown by the light curve, but the third and fourth were partly cloudy, with showers. The growth rate, shown by the heavy black line, rose sharply after the cool morning of June 23, following the light and temperature curves until 10:00 A.M., then dipped slightly, and rose to a second peak at 10:00 P.M. At night the growth rate dropped with the temperature, rising to repeat the day pattern on June 24. The pattern for the showery days of June 25 and 26 is not so clear, but in general growth increased with the temperature in the morning, dropped with the humidity during afternoon, increased with the humidity in the evening and dropped with the temperature after 10:00 P.M. All the effects of day and night can thus be explained on the basis of two indirect effects of sunlight—temperature,

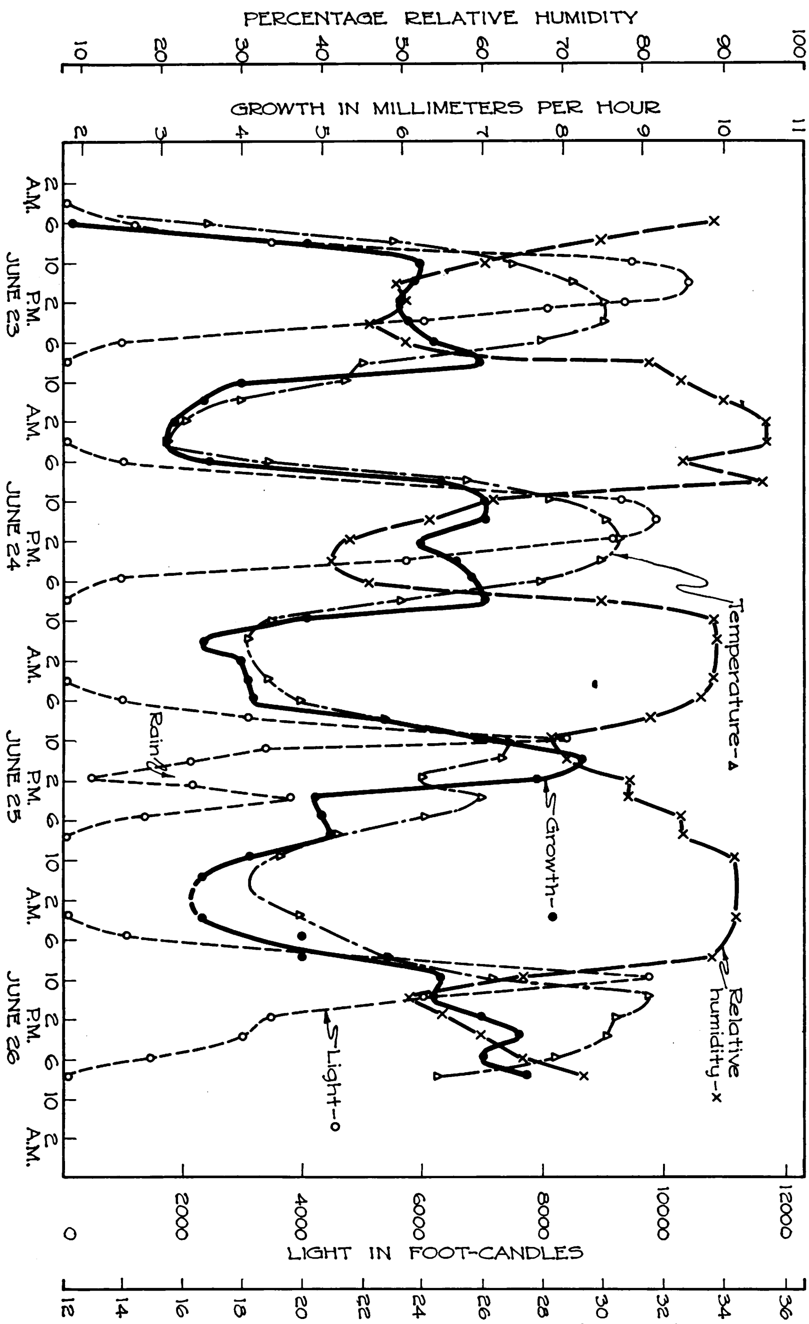

Fig. 1. Light intensity, temperature and relative humidity in relation to the height growth of *Zea mays* under favorable moisture conditions.

and water deficit—the latter as partially expressed by a falling relative humidity, and no direct effect on the growth of this plant is apparent. On June 24, for example, maximum growth rates were reached with full summer sunlight between 10:00 A.M. and 12:00 M. In individual plants this same phenomenon was encountered frequently. Sunlight intensities of 12,000 fc, obtained with banks of reflecting clouds to the north, did not check growth of *Zea mays* when temperatures were below 30° C. and soil moisture and relative humidity were high. Minimum soil moisture percentages during this experiment were above 22 per cent. in a soil with a wilting percentage of 9 to 10 per cent.

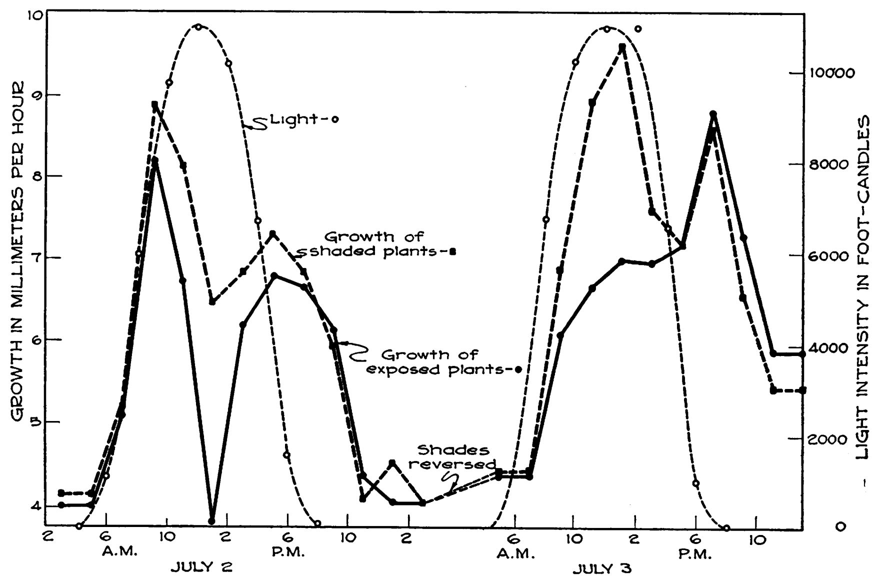

FIG. 2. Light intensity in relation to the growth of shaded and exposed plants of *Zea mays*.

These field results contrast with growth rates of well watered potted plants in the greenhouse (**11**) by showing much higher midday readings. Greenhouse humidities tended to be lower and temperatures higher with the same sunlight, but it seems probable that the restricted root systems of pot-grown plants were less effective in supplying moisture rapidly to the top than were the ramified, well developed root systems of the field plants growing in a deep, well drained soil.

EXPERIMENTS WITH SHADING.—Celotex boards were set to exclude direct sunlight from leaves of one set of six plants in a second experiment. The plants were otherwise fully exposed to north light and to air movement. The growth of these shaded plants, and of a second set exposed normally, is compared with the curves for sunlight and for temperature in figures 2 and 3. The two growth curves were essentially identical except for the greater growth of the shaded plants during the drier part of the day.

Considering the effect of light alone (fig. 2), the growth curves rose with light on the morning of July 2 and then dropped sharply at 1:00 P.M. Growth of the shaded plants rose somewhat higher and dropped to a minimum of 6.5 mm. per hour compared to 3.9 mm. for the exposed plants. Evening and night growth rates were obviously unrelated to light since growth increased rapidly between 1:00 and 5:00 P.M. and then dropped to a low value in the late evening. The shades were reversed at daylight on July 3, and the effects of the previous day's shading apparently reduced the morning growth rates of the newly exposed plants. The shaded plants made their maximum growth at 1:00 P.M., dropped to a daytime low at 5:00 P.M. and rose sharply with the unshaded plants to a second high at 7:00 P.M., just before sunset.

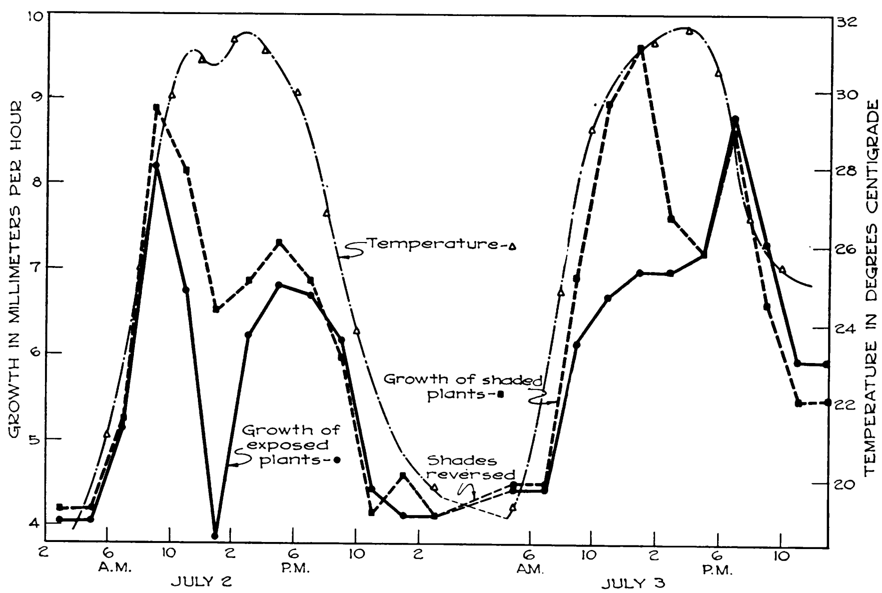

FIG. 3. Temperature in relation to the growth of exposed and shaded maize plants.

When these growth curves are compared with the air temperature curve (fig. 3), growth is seen to have followed temperature closely except during the driest part of the day, when the growth of the exposed plants was reduced more than that of the shaded ones.

Water deficits were measured directly in the shaded and unshaded plants by an eosin absorption method. Extra plants were shaded with celotex board for the measurements, and six control and six shaded plants were cut at two-hour intervals. The plants were immediately recut under water to eliminate plugging of the xylem by air, transferred to an eosin solution for 20 seconds, the top of the stalk cut away to stop intake of the dye, and the base split to measure the upward movement of the dye. With practice, dye absorption time could be controlled within one second and concordant results obtained. Maximum rates of dye movement shown in figure 4 are over 100 cm. per min., and rates of nearly 200 cm. have been observed. These figures do not represent normal rates of water movement in the plants, which usually are estimated in centimeters per hour, but indicate a sudden movement of water through the xylem and into the parenchyma of the plant when tension is released at the bottom of the columns. With dewfall, night-time dye absorption drops to zero, and midday readings of 6 cm. per min. were obtained by holding cut plants in water and shade for 30 min. before transferring to the dye.

In figure 4 the eosin injection figures are inverted, as records of water deficits within the plants, and plotted above the growth curves. In general they explain the failures of the growth curves to follow the temperature (fig. 3). The greater eosin uptake and lower midday growth rate of the

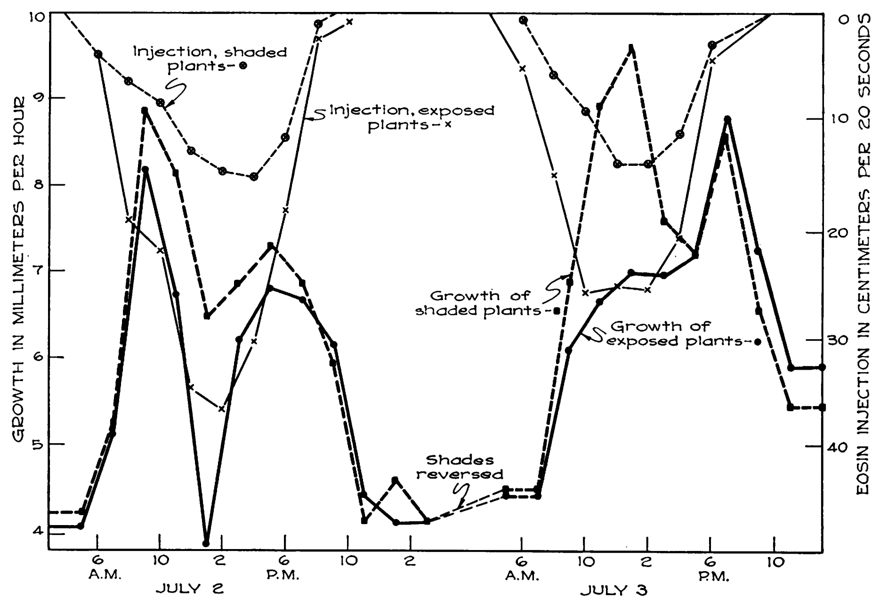

Fig. 4. Eosin injection, as a record of internal water deficit, and growth of maize.

unshaded plants on July 2 is explained as due to the drying effects of a brisk southwest wind. The later and higher growth peak of the shaded plants on the second day is not reflected in the injection curves and may have been due to chance, or to failure of the cut plants to show accurately the conditions within the nearby growth block.

This experiment also indicates that temperature is the main controlling factor for elongation in maize, with water deficit the opposed factor. When moisture did not become limiting, the growth rates shown in figures 1 and 3 doubled for temperature increases of 10° C. between the limits of 15° and 30°. Earlier and unpublished work (**8**, **11**) indicates that 10° C. is the minimum for growth of maize and that 30° is near the optimum.

In a second shading experiment six plants were covered with heavy paper until maximum light intensities were 1 to 3 fc. The first day after shading the covered plants grew four times as fast as the controls between 12:00 M. and 2:00 P.M., but the daily total for the two groups was the same, the control plants having made a much greater evening growth. By the third day of continuous darkness, growth of the covered plants began to slow from starvation, shown in low sugar percentages, dropping to less than 1 mm. per hour on the fifth day, while growth rates for the controls varied between 2 and 9 mm.

EFFECTS OF DRIER WEATHER.—If the midday dip in growth rates is the effect of water deficits, and the night time drop is due to low temperatures, hotter, drier weather should increase the night and decrease the daytime growth rates until the classical picture of plants growing at night is obtained. An approach to such a record was obtained on July 12–13 (fig. 5) when the maximum temperature was 37° C., the minimum 24.5°, and the soil moisture immediately under the hills was 3 to 4 per cent. above the wilting point. Moisture midway between hills was 4 per cent. higher and near the field capacity. DAVIS (**5, 6**) has shown, however, that soil moisture near the plant is removed preferentially, even when as here, fully developed root systems are present in moist soil farther away, and that soil moisture percentages well above the permanent wilting point may sharply check the growth of rapidly transpiring plants.

On July 12 the growth of maize, as shown by the heavy line in figure 5, dropped in the morning until the rate at 2:00 P.M. was about one-third of that at 6:00 A.M. The relative humidity was no lower than on June 24 (fig. 1) when the 2:00 P.M. growth rate was nearly five times as great. The eosin injections, however, showed a considerably greater internal water deficit in the slowly growing plants, with a figure of 44 cm. in 20 seconds at 2:00 P.M. of July 12. Temperatures, too, were probably excessive, although it is difficult to distinguish between the effects of high temperatures and high internal water deficits under field conditions. By 8:00 P.M. the temperature had dropped to 30° C., the eosin injection to 5 cm., and the plants were growing at a rate of 8 mm. an hour. By midnight the rate was down to 5.5 mm., dropping with the temperature and possibly with the completed elongation of an accumulation of freshly divided cells. The daytime pattern of July 13 was essentially the same as that of July 12 except that partial cloudiness maintained the 2:00 P.M. minimum at a higher rate. The night temperature, however, was 8° or 9° C. below that of the previous night, and the night growth rate was down to less than half. Also the growth rate rose with the temperature on the morning of July 14. The actual rates, however, were nearly identical with those obtained at the same time and with the same temperature on the previous day. July 14 temperatures were not excessive, and the poor daytime growth is explained again by the eosin injection figures which reached the high value of 35 cm. by 10:00 A.M. These plants showed no tendency to wilt at any time during the experiment; the soil moisture did not reach the wilting percentage under the hills, and the second foot of soil between the hills, well filled with roots, was still near field capacity at the end of the experiment.

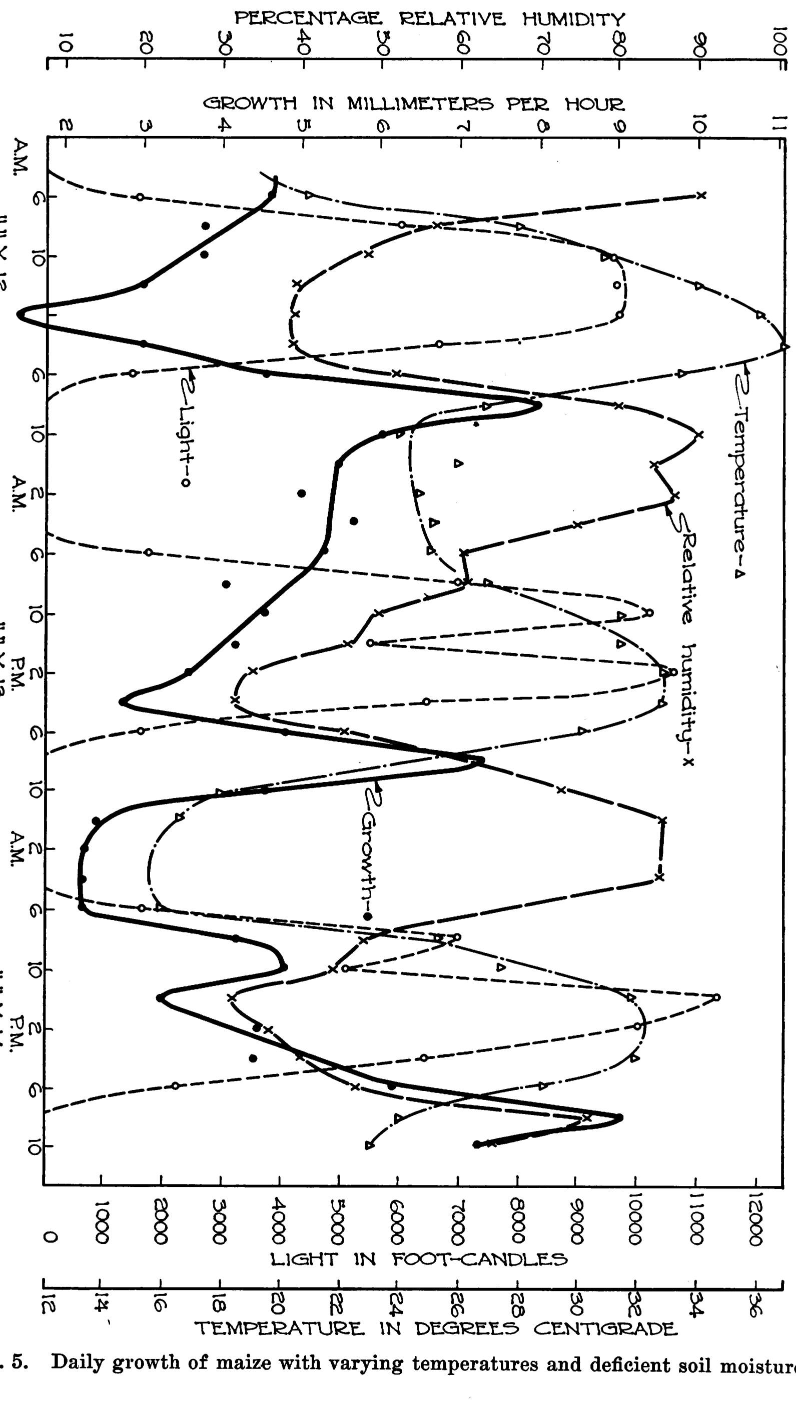

FIG. 5. Daily growth of maize with varying temperatures and deficient soil moisture.

Experiments with other plants

The data obtained with *Zea mays* seem clear cut. At temperatures between 10° to 15° and 30° to 35° C. the normal height growth of this plant was determined by temperature and internal moisture supplies. Light of the qualities and intensities obtained in Iowa sunlight had no direct effect upon its growth, although the indirect effects through photosynthesis, temperature, and transpiration are of major importance. Because the growing regions of the maize plant are thoroughly shielded from the direct action of the shorter wave lengths of sunlight, other, more exposed, plant organs were measured in further tests of the effect of light on growth.

Asparagus.—The growing points of young shoots of asparagus (*A. officinalis*) are more nearly exposed to direct sunlight, although they too are

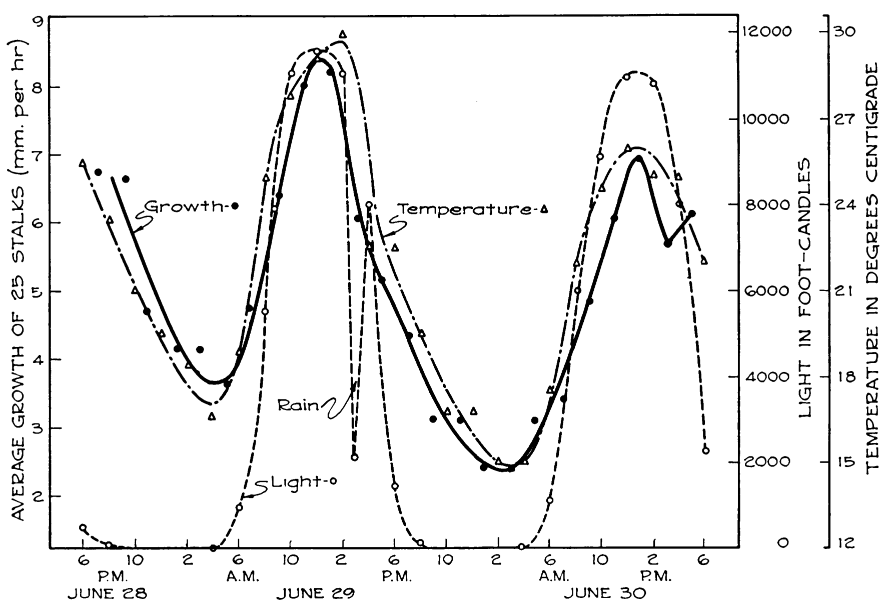

Fig. 6. Light intensity and temperature in relation to the growth of asparagus.

covered by layers of scale leaves. The young shoots differ from maize also in exposing very little transpiring surface. Stakes were driven by each of twenty-five actively growing young shoots of asparagus and their heights measured from this base at two-hour intervals over a 48-hour period. Average hourly growth rates, light intensities, and temperatures are plotted together in figure 6. The dependence of the growth of this plant upon temperature during this moderately warm, moist period is obvious from the data. These results agree with those of Culpepper and Moon (**4**) and Working (**23**). No inhibiting effect of light can be detected, and the growth of ten plants shaded with insulating board was not significantly different from that of the exposed plants.

Bindweed.—The growing points of the vine *Polygonum convolvulus* are only lightly covered by young leaves at the tips of stems about 1.0 mm. in diameter. The meristems are thus well exposed to the direct effects of sunlight. Ten wild plants of this weed were marked and measured at four-hour intervals. Plants were some 80 cm. in length and just beginning to fruit at the start of the experiment. Although a full complement of leaves was exposed to full sun with slowly drying soil, Polygonum plants showed no evidence of an internal water deficit (fig. 7). Neither did they show any inhibiting effect of sunlight. Growth followed the temperature curve with the exception of the 2:00 to 6:00 P.M. jump on July 11. The four days shown were successively hotter and growth was successively less. Watering and shading, however, failed to restore the growth rate which continued to drop, apparently as a correlative effect of fruit production.

CASTOR BEAN.—The expansion of young leaves of *Ricinus communis* would seem to be a growth process particularly susceptible to inhibition by

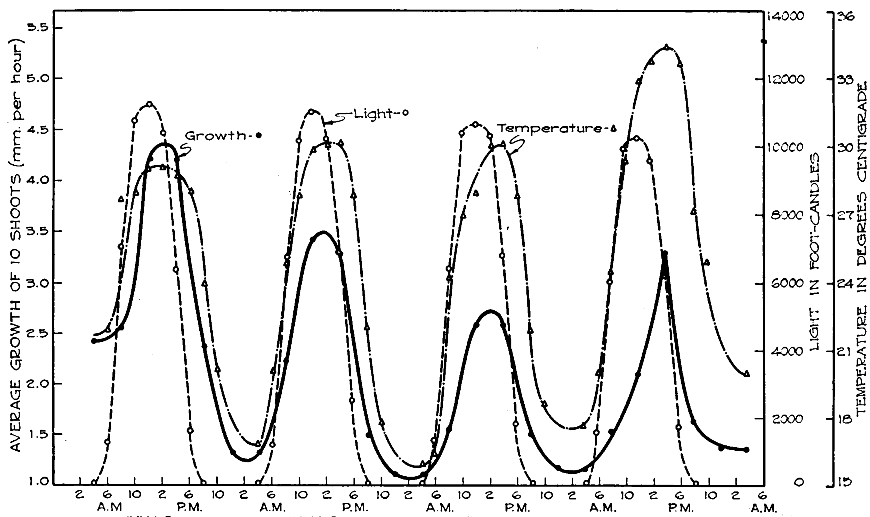

FIG. 7. Light intensity and temperature in relation to the growth of shoots of *Polygonum convolvulus.*

light. The thin blade tissue is fully exposed to any possible chemical as well as physical effects of sunlight, and the radiation might be expected to affect the formation, distribution, or action of growth hormones in the leaf (**1**), or possibly to act directly to speed up the differentiation processes (**10**) and thus check cell enlargement. The results shown in figure 8 are therefore somewhat surprising, for fully exposed leaves in bright July weather showed the same type of curves obtained with growing maize plants in June. Growth in width of these leaves rose with the temperature in the morning, dipped at midday with a water deficit, partially expressed by the relative humidity, rose again in the evening to drop again with the night temperature. Morning growth rates reached a maximum between 8:00 and 10:00 A.M. on July 23 (plotted at 9:00 A.M.) but 8 of 25 leaves made their greatest growth between 10:00 A.M. and 12:00 M. when the sunlight intensity ranged from 10,000 to 11,000 fc. When allowance is made for the effects of decreased turgor in the expanding cells, it hardly seems possible to assign any additional inhibiting effect to sunlight.

One point in this experiment may be of special interest. With a random sample of young leaves large enough for their maximum width to be measured conveniently, and with growth rates of 2 or 3 mm. an hour, final leaf sizes ranged up to 40 cm. "Growth" in these large leaves, and possibly in all this material, was probably due to cell enlargement alone. There was no indication that growth rates in the larger leaves were quantitatively or qualitatively different from those in leaves of less than 10 cm. Cell enlargement generally is considered to be a physical process of water absorption, and as such should have a temperature coefficient of 1+. Instead, the coeffi-

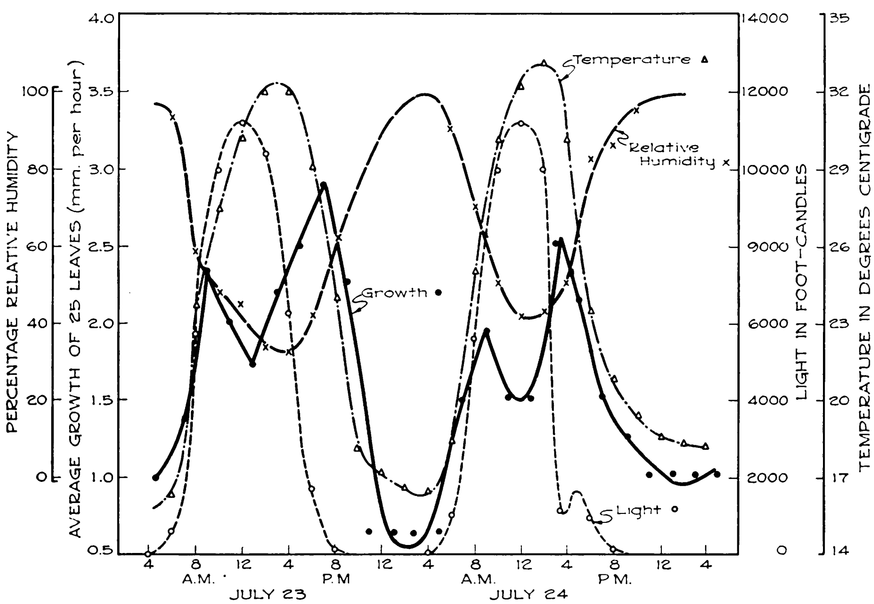

FIG. 8. Light intensity, temperature and relative humidity in relation to the expansion of leaves of *Ricinus communis*.

cients were very clearly 2+. Such results might be explained by assuming that the chemical formation and action of auxins in increasing cell wall plasticity is the major limiting factor in cell expansion, and that water supplies and turgor pressure are only secondary. If temperature is effective upon both cell division and cell enlargement, the close dependence of size increases upon temperature, shown throughout these experiments, is more easily explained.

Summary

Measurements of the combined elongation of the central axis and a young leaf of *Zea mays,* of the axis alone of *Asparagus officinalis* and *Polygonum convolvulus,* and of leaf blade expansion in *Ricinus communis* were made on field grown plants. In most of these plants the combined effects of cell

division and enlargement were included in the "growth" measurements, but in the larger leaves of the castor bean it is probable that cell expansion alone was concerned.

All measurements of both axes and leaves showed a tendency for size increases to follow the temperature curve, and thus, other factors being equal, to be *increased* in sunlight. Growth was checked, however, by water deficits within the plant. Such deficits are generally inversely proportional to the relative humidity and the available soil moisture, and directly proportional to light intensity, temperature, and air movement.

In numerous individual measurements maximum growth of both axes and leaves was obtained with full exposure to sunlight at 10,000 fc or more. Readings were made with a Weston photocell, and intensities as high as 12,000 fc, obtained with clear sun and reflecting banks of cumulus clouds, did not appear to be directly inhibiting for growth. No measurements of ultraviolet radiation were made, but, with the generally high relative humidities (50 to 60 per cent.) prevalent at the time these readings were taken, it is probable that values for this fraction were low, particularly in the shorter wave lengths which have been shown to be directly inhibiting (**12**, **16**).

Full Iowa summer sunlight does not appear to have any direct effect upon growth of plants. Indirectly it increased growth by increasing photosynthesis and raising the temperature. Growth was decreased by excessive temperature and by internal water deficits developed in plants under the combined effects of sunlight, high absorptive capacity of the air and decreasing soil moisture percentages. Field grown plants were less subject to internal water deficits with high soil moisture than greenhouse plants in pots. The roots of field plants probably develop a greater absorptive area. Water near the plants was used preferentially, and sharp daytime checks in growth were observed when the principal absorption was occurring two feet from the base of plants with roots three feet or more long.

Experiments indicating that the expansion of large leaves has the temperature coefficient of a chemical reaction suggest that the action of auxins in increasing the plasticity of expanding cells may be more important than turgor pressure in cell enlargement.

The plants investigated made a greater growth in the daytime when temperature was the limiting factor, and a greater growth at night when moisture was limiting. Very commonly the interaction of these two factors produced a double peak of early morning and evening growth.

IOWA STATE COLLEGE
AMES, IOWA

LITERATURE CITED

1. AVERY, G. S. Jr. Differential distribution of a phytohormone in the developing leaf of Nicotiana, and its relation to polarized growth. Bull. Torrey Bot. Club **62**: 313–330. 1935.

2. BROWN, W. H., and TRELEASE, S. F. Alternate shrinkage and elongation of growing stems of *Cestrum nocturnum.* Philippine Jour. Sci. **13C**: 353–360. 1918.
3. COSTER, C. H. Die täglichen Schwankungen des Längenzuwachses in den Tropen. Rec. Trav. Bot. néerl. **24**: 257–306. 1927.
4. CULPEPPER, C. W., and MOON, H. H. Effect of temperature upon the rate of elongation of the stems of asparagus grown under field conditions. Plant Physiol. **14**: 255–270. 1939.
5. DAVIS, CHARLES H. Absorption of soil moisture by maize roots. Bot. Gaz. **101**: 791–805. 1940.
6. ————. Response of *Cyperus rotundus* L. to five moisture levels. Plant Physiol. **17**: 311–316. 1942.
7. INGE, F. D., and LOOMIS, W. E. Growth of the first internode of the epicotyl in maize seedlings. Amer. Jour. Bot. **24**: 542–547. 1937.
8. LEHENBAUER, P. A. Growth of maize seedlings in relation to temperature. Physiol. Res. **1**: 247–288. 1914.
9. LLOYD, F. E. Growth of Eriogonum in relation to light, temperature and transpiration. Carnegie Inst. Washington Yearbk. **15**: 58–59. 1916.
10. LOOMIS, W. E. Growth-differentiation balance vs. carbohydrate-nitrogen ratio. Proc. Amer. Soc. Hort. Sci. **29**: 240–245. 1932.
11. ————. Daily growth of maize. Amer. Jour. Bot. **21**: 1–6. 1934.
12. MASON, S. C. The inhibitive effect of direct sunlight on the growth of the date palm. Jour. Agr. Res. **31**: 455–468. 1925.
13. MCCALLA, A. G., WEIR, J. R., and NEATBY, K. W. Effects of temperature and sunlight on the rate of elongation of stems of maize and gladiolus. Canadian Jour. Res. **17**: 388–409. 1939.
14. OSMASTON, B. B. Rate of growth of bamboos. Indian Forester **44**: 52–57. 1918.
15. POPP, H. W. A physiological study of the effect of light of various ranges of wave length on the growth of plants. Amer. Jour. Bot. **13**: 706–736. 1926.
16. ————, and BROWN, FLORENCE. A review of recent work on the effect of ultraviolet radiation upon seed plants. Bull. Torrey Bot. Club **60**: 161–210. 1933.
17. PORTERFIELD, W. M. Jr. A study of the grand period of growth in bamboo. Bull. Torrey Bot. Club **55**: 327–405. 1928.
18. PRANTL, K. Ueber den Einfluss des Lichts auf das Wachsthum der Blätter. Arb. Bot. Inst. Wurzburg **1**: 371–384. 1873.
19. PRESCOTT, J. A. Some observations on the growth of maize in Egypt. Sultanic Agr. Soc. Bull. **7**: 1–25. 1921.
20. SACHS, JULIUS VON. Ueber den Einfluss der Lufttemperatur und des Tageslichts auf die stündlichen und täglichen Aenderungen des

Längenwachsthums (Streckung) der Internodien. Arb. Bot. Inst. Wurtzburg **1**: 99–192. 1872.

21. TRELEASE, S. F. Night and day rates of elongation of banana leaves. Philippine Jour. Sci. **23**: 85–96. 1923.
22. WENT, F. W. Effects of light on stem and leaf growth. Amer. Jour. Bot. **28**: 83–95. 1941.
23. WORKING, E. B. Physical and chemical factors in the growth of asparagus. Arizona Agr. Exp. Sta. Tech. Bull. 5. 86–124. 1924.